From Early Experience in Visual Information Processing in Perceptual and Reading Disorders. Edited by F. A. Young and D. B. Lindsley. Nat. Acad. Sci., Washington D.C., 1970.

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Cerebral Dominance in Perception

This presentation will be concerned largely with a review of some recent evidence obtained by Dr. Ronald Saul and me[4] on the effects on visual perception of congenital absence of the corpus callosum in man. The behavioral symptoms seen with congenital absence of the callosum will be compared with those produced by surgical elimination of the callosum and other cerebral commissures. In the latter case, of course, the two hemispheres, which have functioned together for years with the channels for cross-communication intact, must suddenly get along without the accustomed direct lines for cross-talk. With congenital failure, the hemispheres must get along from the very beginning without the normal cross-communication. The increased functional compensation that is achieved in the congenital situation, compared with that after surgery in the fully developed system, will give us some indication of the degree of functional plasticity that exists in the growing and developing brain, beyond that seen in the fully developed brain.

We have been fortunate during the last year in having available for testing and study a patient (S.K.) recently diagnosed from x-ray studies to have complete agenesis of the corpus callosum. We had seen others in the past, but this particular patient, first seen by Dr. William Wright at the Los Angeles County General Hospital, has one of those very rare

"asymptomatic" cases; no signs of abnormality were discovered until the age of 19, when headaches developed after an acute attack of hydrocephalus. The patient recovered quickly with treatment and returned to college, where she is currently a sophomore with an average scholastic record (C's and B's).

It was our first thought that, even though no functional symptoms had been evident in ordinary behavior, such symptoms associated with loss of the corpus callosum could probably be demonstrated if we could get her into the laboratory and put her through some of the series of tests for interhemispheric integration with which we had been successful in recent years in demonstrating symptoms in surgical patients with cerebral commissurotomy (Figure 1). Normal subjects perform these tests without difficulty, but a group of patients of Vogel and Bogen who have undergone surgical section of the corpus callosum and anterior commissure either fail completely or show gross impairment.[6,8]

Our patient went through every test without hesitation, performing easily and apparently at normal efficiency task after task that had stopped the surgical patients. I will run through a few examples to illustrate the kinds of functions involved, with emphasis on test performances that involve vision and language. These will help to give an idea of the functional reorganization and compensation of the cerebral mechanisms underlying vision and language that are possible in the still developing and growing brain but not in the fully developed brain. This patient exemplifies the functional plasticity of neural maturation[7] that is presumed basic to many phenomena in which early experience is critical in the shaping of adult behavior.

Patients deprived of the corpus callosum by surgery are unable to describe in speech or writing things that they see in the left half-field of vision. Whereas they have no trouble with items in the right half-field, they consistently report that they see nothing when stimuli are presented on the left side of the vertical meridian. In these tests, the visual stimuli are flashed at 1/10 sec or less to prevent the use of rapid eye movements to get the stimuli into the other half-field. With further testing, however, it becomes evident that these commissurotomy patients are able to speak about their inner experiences from one of their hemispheres only—specifically, the left hemisphere, generally dominant in right-handed persons. Other kinds of tests show that, when the major hemisphere reports that it did not see a left-field stimulus, it speaks for itself alone, and that the stimulus was indeed seen and often well com-

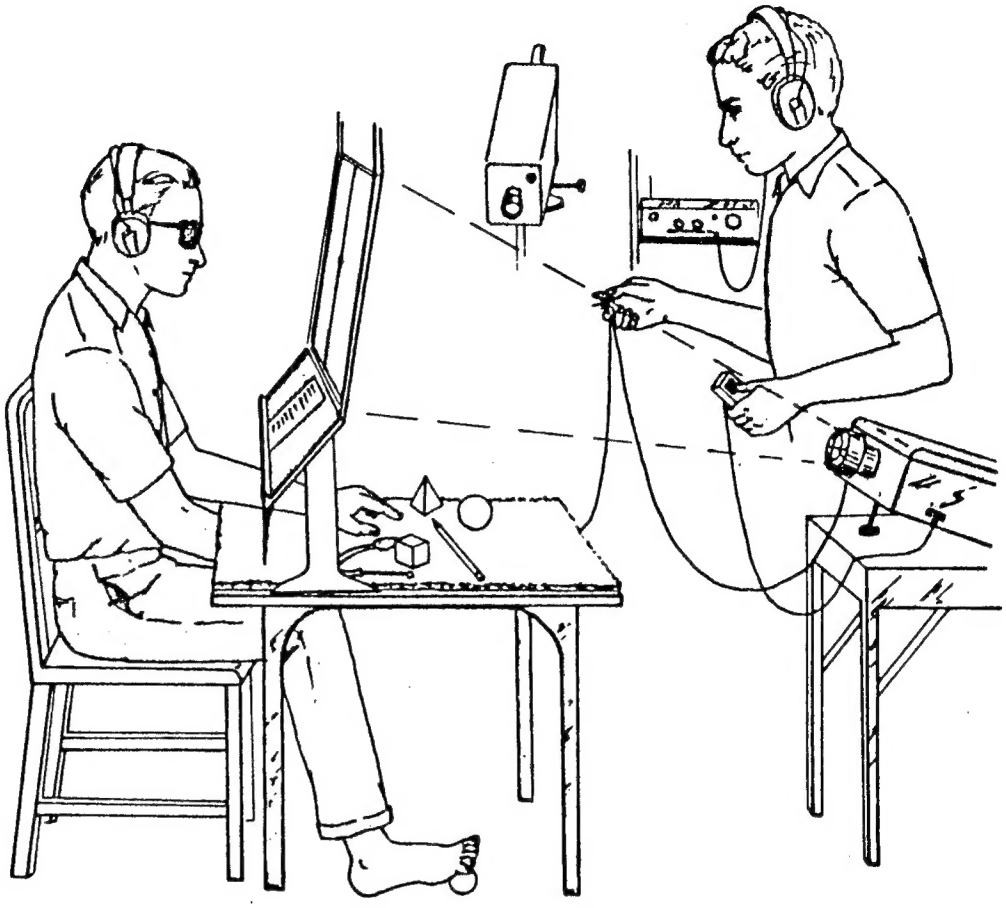

FIGURE 1 Drawing of experimental setup used to demonstrate subject's ability to comprehend a stimulus confined to one visual field.

prehended by the nontalking, the mute, or minor hemisphere. The minor hemisphere's comprehension is expressed in nonverbal tests in which the subject selects the correct name of the stimulus or a matching picture or object by pointing. Ability of the subject to retrieve by touch alone objects pictured in the left half-field and emotional responses to left-field stimuli also show that the left-field stimuli, about which the subject verbally disclaims any knowledge, are actually seen and recognized in the minor hemisphere. Figure 2 shows some of the relationships diagrammatically.

The inner visual world of these subjects has been inferred from such evidence to be double, rather than single, with a separate conscious

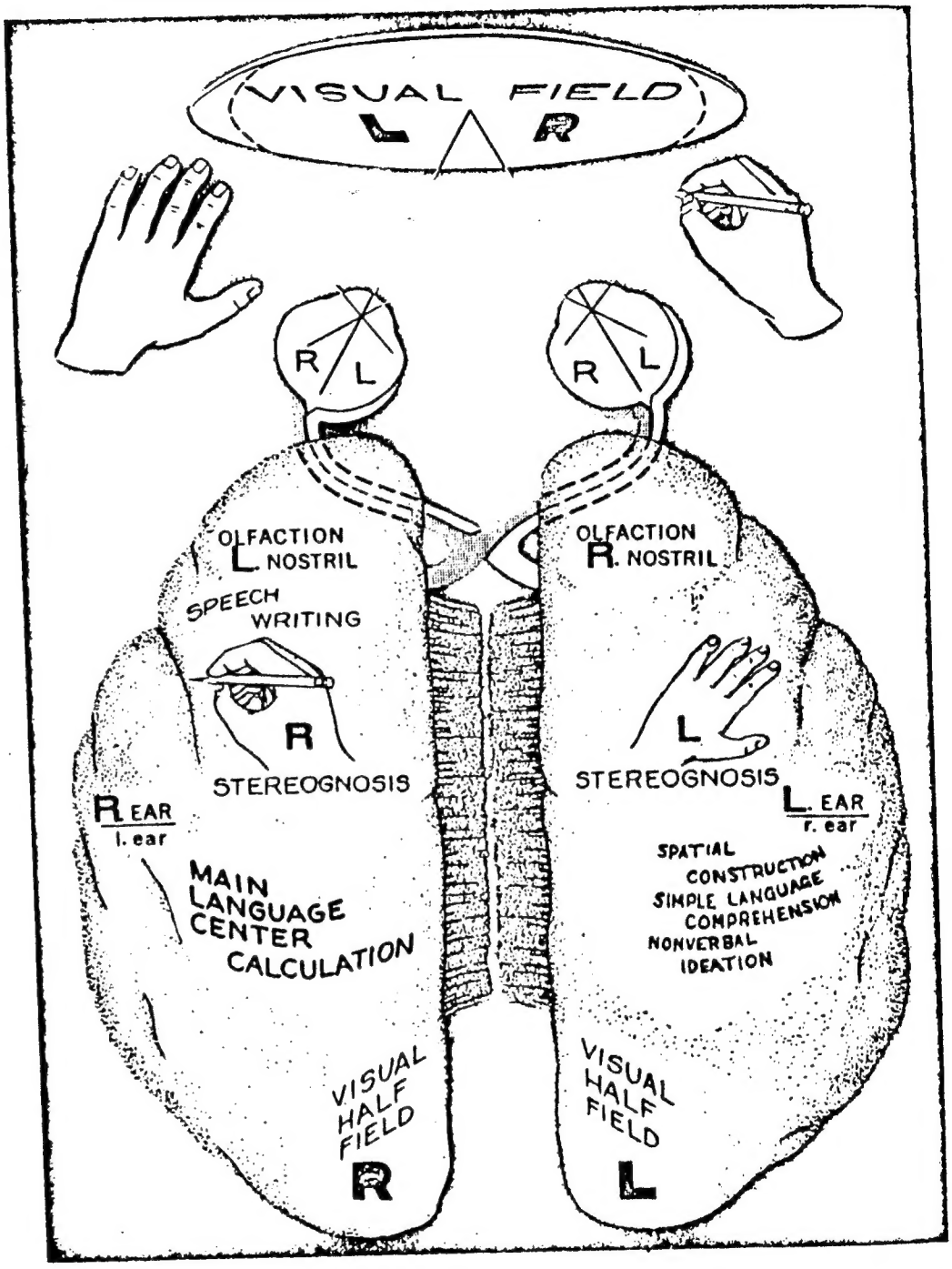

FIGURE 2 Schematic diagram of visual fields, optic tracts, and associated brain areas, showing left and right lateralization in man.

visual awareness in each hemisphere. The right and left inner visual spheres lack their normal conscious connection. A profound absence of awareness in each hemisphere of the mental experiences of the other is consistently evident in the test data. Along with the immediate visual perception, visual memories and all kinds of mental associations of vision with language, with calculation, and with other sensory modes—including touch, hearing, and olfaction—are all confined to the same hemisphere.

No evidence of a similar separation and doubling of inner experience, visual or otherwise, was found in our patient with congenital absence of the callosum. She gave verbal reports from either visual half-field with no hesitation. She was able to read words and numbers across the vertical meridian with no sign that right and left halves were perceived separately. Unlike the surgical patients, she could retrieve with either hand objects seen in either visual half-field. She could add and multiply pairs of numbers shown one in the left and one in the right half-field. In tests involving stereognosis and auditory and olfactory input, she also displayed seemingly normal right–left cross integration.

The extent to which functional compensation has been achieved in this patient's vision is perhaps best illustrated by tests that involved the rapid reading of words presented tachistoscopically, part of the word to the left and part to the right of the vertical midline. For example (see Figure 3), the letters "a b" might fall in the left field for projection to the right hemisphere, and the letters "o v e" in the right field for projection to the left hemisphere. In the same list may be other words like "stout," "only," and "rely," so that the subject cannot use the left or

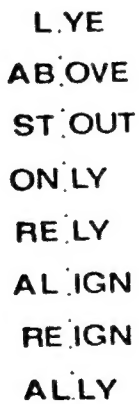

FIGURE 3 List of words used to test subject's ability to integrate stimuli coming from left and right visual fields.

right part of the word to cue in the whole word. Even the pronunciation of a syllable or two seen on one side of the vertical meridian often cannot be inferred without consideration of the rest of the word, on the other side. Both parts of the word must thus be taken into account and integrated into a proper whole. S.K. was able to read these words with the mixed right–left input promptly and as well as with the unified right or left input.

We can see the extent to which callosal compensation had been achieved, but we cannot yet explain it satisfactorily. The radical difference in the functional symptoms produced by congenital and by surgical separation of the hemispheres appears to be a direct reflection of the greater plasticity of the developing nervous system, compared with the fully developed system. The underlying factors responsible are very likely basic to many of the more general phenomena that illustrate the functional plasticity of neural maturation. Any insight into the underlying neural factors in this or any other situation would have importance for the whole field of developmental psychobiology, with wide implications extending into ethology, psychiatry, pediatrics, and other disciplines concerned with the effects of early experience on adult behavior.

To account for the compensation achieved in patient S.K., we had best start by reaffirming the absence of any readily apparent explanation. Her normal or near-normal performance on the tests mentioned remains puzzling and difficult to account for in terms of the anatomy and physiology of known neural pathways. Although the anterior commissure often is also absent in such cases, it appears to be present in this person, judging by her x-rays, and to be slightly enlarged, as is not uncommon among cases of agenesis of the corpus callosum. The extra fibers in the anterior commissure might thus be a contributing factor. However, these extra fibers probably total less than 2% of the missing callosal system and have only indirect cross-connections for many of the functions tested. Accordingly, we must look much further for a full explanation. The hippocampal, posterior, and other cerebral commissures apparently are not subject to hypertrophy in callosal agenesis.[3] In an asymptomatic case examined microscopically by Slager *et al.*,[5] the two hemispheres were found to exhibit an essentially typical cytoarchitecture, except for the missing commissure fibers. The histologic examinations described to date, however, have generally been rough, and they do not rule out the presence of an enrichment and elaboration of

commissures and decussations at midbrain and lower levels.

To account for the observed degree of functional compensation in S.K., it would seem necessary to postulate at least a functional elaboration of brain-stem and perhaps lower cross-connection systems. The thinness of the cerebral aqueduct and the ease with which it becomes blocked make one wonder about the presence of an atypical hypertrophy among the midbrain centers. In addition to a purely functional reinforcement of whatever connection possibilities exist at these lower levels, there might also be purely embryonic reactions associated with the agenesis of the neocortical system that would make for an enhanced development of the older brain-stem systems that handled higher visual, auditory, somatesthetic, and other functions before the neocortex evolved.

Hypertrophy or functional reinforcement of the normally weak ipsilateral sensory projection system would go far to account for the observed compensation. The behavioral results of early, compared with late, hemispherectomy illustrate the capacity for such development in the somatesthetic system. The ipsilateral auditory and kinesthetic components are already highly developed, and their enrichment would seem to offer no problem. To attain an adequate ipsilateral function in the visual mode would pose the greatest problem, and for present purposes we can focus on the observed visual cross-integration and possible explanatory factors.

The observed ability of S.K. to rapidly read words that fall partly in one half-field and partly in the other seems to imply that the ipsilateral half-field had become projected into the same hemisphere as the opposite half-field. It follows that both half-fields must be closely integrated with speech, also in the same hemisphere. Possible anatomic pathways for this are not easy to see.

One remotely possible pathway for such cross-integration is the anterior commissure. This commissure cross-connects the temporal lobes that are known to be involved in vision. The route is indirect, however, and it is unlikely that the requisite sensory information could be transmitted in sufficient detail to permit one hemisphere to read letters projected from the other hemisphere through the anterior commissure.

Better possibilities probably can be found in cross-connections at midbrain levels associated with visual function in the superior collicular, pretectal, and pulvinar systems.[9] Before evolutionary development of

the neocortex, the midbrain systems carried out visual integration at the highest levels. The upper levels of midbrain vision in present mammals are difficult to assess because of close interaction with the neocortex and dependence on cortical connections. In any case, it is important that visual deficits produced by neonatal removal of occipital lobes are much smaller than those produced by adult removal.[10] We are speaking here mainly of the focal identifying type of vision, rather than the orientational sort more characteristic of the midbrain in the cortically intact mammal.

Assuming that a latent potential for high-level focal vision in the midbrain may be evoked by agenesis of the callosum, as well as by early cortical damage, there would still remain the problem of getting the refined pattern information for reading small letters across the midline, up to the cortex, and integrated with the contralateral information for a verbal readout.

In our latest tests for visual cross-integration, I have used only two- and three-letter words, in an effort to avoid the variables introduced by peripheral vision. The initial scores of S.K. under these conditions show an encouraging difference between the lateral unified input and the mixed or combined right–left input, indicating that in these near-threshold performances that might separate midbrain from direct cortical channels she handles the left-field input better than either the right-field or the combined right–left input.

The question arises of whether speech is bilateralized in this patient. Conclusive evidence is lacking. She is ambidextrous to a high degree, as is often the case in patients with agenesis of the callosum. For example, she writes mainly with her left hand, but she uses scissors better with her right hand. Some preliminary evoked-potential records taken during visual performance suggest that only her left hemisphere is active in vision. It is conceivable that speech, somatesthesis, audition, and vision are all handled in a single dominant left hemisphere. This fits with the findings on near-threshold reading of words from combined right- and left-field input.

Regardless of whether speech is bilateralized or is developed only in a dominant hemisphere, there are indications that in S.K. speech has been developed at the expense of other mental faculties, such as spatial perception. After we had established the lack of functional deficits in the regular series of tests used to demonstrate cross-integrational symptoms after commissurotomy, we started to administer other types of

tests—more generalized tests aimed at the upper limits of various mental and sensorimotor faculties, regardless of lateralization, following the approach of Jeeves.[1] The results to date are only suggestive, but they begin to point to subnormal function in a number of nonverbal capacities. S.K. fairly consistently does better on verbal tasks than on performance or perceptual tasks. She also draws poorly and has difficulty with geography, block design arrangements, and matching patterns—all specialties of the minor hemisphere in typical right-handed persons.

At this stage, our evidence suggests a distinction between two somewhat different types of cross-integrational functions mediated by the corpus callosum: those which can be compensated for in congenital absence of the corpus callosum and those for which compensation is more difficult or impossible. The kinds of functions for which compensation is achieved involve the more direct sensory and motor cross-integrations that were carried out at subcortical levels before evolution of the neocortex. When the neocortical system for vision, normal stereognosis, and other functions evolved, their cross-integrational mechanisms also had to be moved upstairs. The kinds of cross-integrational functions for which compensation is not so easily achieved are those associated with cerebral dominance and the lateral differentiation of higher mental faculties that is peculiar to the human brain. Particularly affected are performances that depend on the mental faculties specialized in the minor hemisphere.

If S.K. has double speech—that is, bilateralized development of speech in both hemispheres—or if speech in her dominant hemisphere has no direct cross-communication with the other hemisphere, the results are much the same. In either case, there is a handicap in that the verbal activities cannot be so well reinforced by functions for which the minor hemisphere is normally specialized, owing to lack of cross-talk in the former case and to intrahemispheric competition in the latter. These functions of the minor hemisphere seem to include spatial and orientational activities, abstract thinking, and creative mathematical and geometric abilities, all of which normally would cooperate with and embellish the verbal hemisphere through the corpus callosum. It is pertinent that, according to the literature, even the least symptomatic subjects with agenesis of the corpus callosum have not been brilliant or even above normal in intellect. The current view is that they attain mediocre intelligence at the most, although they may be highly verbal and even multilingual.

The interpretation that loss of the corpus callosum prevents reinforcement by minor hemisphere functions fits also with results of some recent work.[2] We have considerable evidence that the functions of the minor hemisphere are sufficiently different in kind from those of the major hemisphere that the two tend to conflict and interfere with each other, making it a real advantage to put the two types of activity in separate hemispheres. The minor hemisphere seems to be a specialist at configurational, spatial, synthetic, and geometric activity, whereas the major hemisphere is specialized for sequential, verbal, logical, and analytic activity. The two functions do more than compete for brain space in evolution; the basic difference in the nature of their organization means that excellence in one tends to interfere with top-level performance in the other. On the basis of evidence collected from patients with congenital and surgical absence of the corpus callosum, as well as from the literature, this fundamental antagonism in the nature of these modes of brain functions might be a causal factor behind the evolution of cerebral dominance and lateral specialization in the human brain.

What meaning this may have for problems of dyslexia remains to be seen. One wonders whether a possible factor in dyslexia is an overly strong or extensive, perhaps bilateral, development of the verbal, major-hemisphere type of organization that tends to interfere with an adequate development of spatial gnosis in the minor hemisphere. The facts that general verbal capacity tends to be good in dyslexics and that the frequency of dyslexia is higher among left-handed persons would fit such an interpretation. Extra training in spatial gnosis with special reference to alphabet patterns and the troublesome letters and words subject to directional reversals would seem a natural approach to these problems.

Original work reported here was supported by U.S. Public Health Service grant MH 3372 from the National Institute of Mental Health and by the F. P. Hixon Fund of the California Institute of Technology.

REFERENCES

1. Jeeves, M. A. Agenesis of the corpus callosum—physiopathological and clinical aspects. Proc. Aust. Assoc. Neurol. 3:41–48, 1965.
2. Levy-Agresti, J., and R. W. Sperry. Differential perceptual capacities in major and minor hemispheres. Proc. Nat. Acad. Sci. USA 61:1151, 1968.

3. Loeser, J. D., and E. C. Alvord, Jr. Agenesis of the corpus callosum. Brain 91: 553–570, 1968.
4. Saul, R. E., and R. W. Sperry. Absence of commissurotomy symptoms with agenesis of the corpus callosum. Neurology 18:307, 1968. (abstract)
5. Slager, U. T., A. B. Kelley, and J. A. Wagner. Congenital absence of the corpus callosum. New Eng. J. Med. 256:1171–1176, 1957.
6. Sperry, R. W. Mental unity following surgical disconnection of the cerebral hemispheres, pp. 293–323. In The Harvey Lectures. Series 62 (1966–67). Harvey Society of New York. New York: Academic Press, 1968. 364 pp.
7. Sperry, R. W. Plasticity of neural maturation, pp. 306–327. In M. Locke, Ed. The Emergence of Order in Developing Systems. 27th Symposium of the Society for Developmental Biology. Supplement 2. New York: Academic Press, 1968. 350 pp.
8. Sperry, R. W., M. S. Gazzaniga, and J. E. Bogen. Function of neocortical commissures: syndrome of hemisphere deconnection. In P. J. Vinken and G. W. Bruyn, Eds. Handbook of Clinical Neurology. Amsterdam: North-Holland, 1969.
9. Trevarthen, C. B. Two mechanisms of vision in primates. Psychol. Forsch. 31:299–348, 1968.
10. Wetzel, A. B., V. E. Thompson, J. A. Horel, and P. M. Meyer. Some consequences of perinatal lesions of the visual cortex in the cat. Psychon. Sci. 3:381–382, 1965.

DISCUSSION

DR. INGRAM: I suggest that the dyslexic individual is faced with several problems in addition to the spatial relationships that he cannot visualize. He also requires some teaching in terms of auditory concepts, because this function is in the hemisphere that is functioning best and that should be concentrated on.

DR. MASLAND: Dr. Ingram has suggested that there is a very important additional element in the problem of reading. It is not merely a matter of recognizing the shape of an object, but the establishment of an association between the shape of an object and a verbal sound information element. That function has already been established in the left hemisphere of the average child, and it seems to me that the fundamental problem of the dyslexic child, particularly the child who is having letter reversals, is the necessity of establishing a relationship between a visual spatial function, which is most likely mediated in the right hemisphere, and a language function, which has already been established in the left hemisphere. The problem is to develop techniques whereby spatial functions are dissociated from the language functions of the left side.

DR. INGRAM: There is a possibility that this dyslexic schoolchild would be taught by the so-called "look and say" method. I think that would be disastrous. This child has to be taught to relate the visual symbol, as Dr. Masland says, to the spoken syllable. I think by the stage of learning to read the child is probably able to recognize the visual symbol, but not to relate it to the auditory symbol. Therefore, you have to work with a phonic approach, and establish the phonic relationships. I am trying to point out that it is difficult to short-circuit a function that you think is not there.

DR. SPERRY: I was referring specifically to the perception of spatial relations during early learning of reading and writing, when letters and words tend to be reversed, and did not mean to imply a general application to reading aloud and to all forms of dyslexia.

DR. MASLAND: Maybe it is unwise to generalize, but for a person to learn to read, obviously he has to have the ability to see, he has to be able to analyze and recognize the material being seen, and he must be able to associate that object with an auditory symbol.

DR. BERING: The auditory counterpart is not necessary. It has been brought up here that people can learn to read without it if the hemispheres are intact. There are auditory and spoken relationships with reading, but neither is absolutely necessary.